# LIASSIC PLESIOSAUR EMBRYOS REINTERPRETED AS SHRIMP BURROWS

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ABSTRACT. A peculiar nodule from the Upper Liassic (Toarcian) shales of Whitby, Yorkshire, is interpreted as an infilled burrow system which was probably excavated by a shrimp-like crustacean (possibly *Glyphea* sp.). This interpretation is supported by comparisons with fossil crustacean burrows in the ichnogenus *Thalassinoides*. The nodule had formerly been regarded as a cluster of fossil embryos from the aquatic reptile *Plesiosaurus*.

IN September 1887 H. G. Seeley delivered four reports on fossil reptiles to the British Association meeting at Manchester. Three of those reports dealt with anatomy and systematics, but the fourth concerned the more unusual subject of fossil embryos. Seeley described and exhibited a peculiar nodule showing supposed embryos of a Jurassic plesiosaur—an aquatic reptile of the suborder Plesiosauria (order Sauropterygia). His account of the embryos was summarized the following year (Seeley 1888), though a full description did not appear until 1896.

Seeley's plesiosaur embryos have attracted little attention: they have never been figured, and it is difficult to find more than passing mention of them in the literature of vertebrate palaeontology. They were briefly noticed by Woodward (1898, p. 161), Williston (1914, p. 94), and de Saint-Seine (1955, p. 422), but seem never to have been re-examined in detail. Abel's classic work *Vorzeitliche Lebensspuren* (1935) devoted much attention to embryos and neonates of ichthyosaurs (reptile order Ichthyosauria), but made no mention at all of plesiosaur embryos. There has often been speculation about the mode of reproduction in plesiosaurs (see, for example, Robinson 1975), but the embryos described by Seeley seem to have been overlooked.

This paper provides the first illustrations of the supposed plesiosaur embryos, and offers a reinterpretation of these curious fossils.

## MATERIAL

The material described by Seeley was acquired in 1909 by the British Museum (Natural History), where it is now catalogued as R 3585. It comprises: an irregular nodule of pyritic mudstone and shale, approximately $11 \times 8 \times 8$ cm (text-fig. 1); a small fragment, broken from the main nodule; five slides, each with a thin section; a slide with twenty-three stained serial sections from the neck region of a modern lizard embryo. The small fragment was detached in Seeley's search for internal structure, and it provided material for the thin sections; the serial sections of the lizard embryo had been obtained for comparative purposes (Seeley 1896, p. 21).

The nodule almost certainly came from coastal exposures of the Upper Lias (Whitbian sub-stage of the Toarcian) near Whitby, Yorkshire. Seeley received the nodule in 1887 from J. F. Walker (then curator of the Yorkshire Natural History Society), who had obtained it from a dealer in Whitby. The Whitby fossil-dealers were not averse to importing their wares from the Lower Liassic of Lyme Regis, Dorset, but probably did so only in the case of exceptionally fine and valuable specimens (notably fossil fishes; see Blake 1876, pp. 257–259). The Liassic shales near Whitby are rife with oddly shaped concretions and nodules (Hallam 1962; Howarth 1962), and it seems unlikely that a dealer would have imported an example from Dorset when so many were to hand locally.

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The Whitby Lias is about 76 m thick, and may be summarized as follows (incorporating data from Hallam 1962; Howarth 1962, 1973; Hemingway 1974):

| Formation | Thickness (m) | Ammonite Zone | Stage |
|---|---|---|---|
| Dogger | (sandstones and ironstones) | | Bajocian |
| unconformity | | | |
| Cement Shales | 5·5 | *Hildoceras bifrons* | Toarcian |
| Main Alum Shales | 22·0 | | |
| Hard Shales | 4·5 | | |
| Bituminous Shales | 23·5 | *Harpoceras falciferum* | |
| Jet Rock Shales | 8·5 | | |
| Grey Shales | 13·5 | *Dactylioceras tenuicostatum* | |

The succession consists of shales, with minor argillaceous limestones and rare seams of siderite mudstone. Nodules and concretions are extremely abundant; some are scattered at random through the shales, while others occur in constant bands which serve as useful marker horizons (see Howarth 1962). Concretions in these marker horizons often have highly distinctive shapes, and have been named accordingly—'cannon balls', 'cheese doggers', 'curling stones', 'pseudovertebrae', and so on. Unfortunately the nodule described by Seeley cannot be referred with certainty to any of these marker horizons. Seeley's specimen has a matrix of soft, grey, flaky, and non-bituminous shale, and is unlikely, for that reason, to have been obtained from the zone of *Harpoceras falciferum*—where the shales are usually brown in colour and often have a characteristic 'oily' smell. Nor is it very likely that Seeley's specimen came from the Hard Shales or the Main Alum Shales: in many places these shales weather to a brown or reddish colour, and they sometimes produce efflorescent alum. The specimen probably originated from the Grey Shales or the Cement Shales.

## DESCRIPTION

The supposed plesiosaur embryos are rounded masses of grey-brown mudstone protruding from a core of flaky grey shale (text-fig. 1). The shale is very soft, and contains tiny blebs and veins of white calcite, together with occasional flecks of black plant material. The bodies of the embryos are slightly harder than the shale matrix, extremely fine-grained, and rich in finely divided pyrite. Seeley originally believed the embryos to be phosphatic (1888), but later determined that they were in fact pyritic (1896). The embryos, and some areas of intervening shale, have a greasy lustre which has probably been enhanced, if not produced, by repeated handling of the specimen.

Seeley identified and numbered four principal embryos, with 'indications of three or four others' (1896, p. 20). His numbering is still visible on the specimen, in faded red ink, and will be followed here (see text-fig. 2). For the sake of brevity I will also adhere to Seeley's descriptive terminology (e.g. the 'head' of embryo 1, the 'limbs' of embryo 3, and so on); and to assist my discussion the specimen will be oriented as a spheroid with the 'head' of embryo 1 directed to the 'North Pole'.

Seeley's description (1896) is both detailed and accurate and need not be repeated here. However, the specimen has certain features that were not mentioned by Seeley. First, it is badly damaged in the region of the 'North Pole', where it seems that several large flakes have been removed by hammer blows (text-figs. 1A, 2A). The fragment detached to provide thin sections was clearly the last piece to be removed, for it can still be fitted on to the main nodule, where it forms part of an older fracture-scar. In some places the specimen appears to have been subjected to rather rough mechanical preparation; there are, for example, very deep needle-marks along the right side of the 'neck' in embryo 1.

The embryos are clustered in a partly overlapping arrangement; the 'neck' of embryo 3, for example, is largely concealed by the 'body' of embryo 1. Elsewhere one embryo may be joined to another without the slightest trace of a dividing line (see text-fig. 1B). The arrangement of the supposed embryos is not entirely random: they extend in a radiating pattern, along meridians, when viewed from the 'South Pole' (text-fig. 2B).

Seeley could find no definite trace of organic structure in the specimen, and his identification of 'embryonic plesiosaurs' rested almost entirely on the criterion of shape. He considered that embryo 1 showed 'the head, neck, body, tail and limbs of such a shape as a plesiosaur would show', and pointed out that the other embryos were basically similar in form; differences in shape between one embryo and another were taken to reflect 'various stages of development' (Seeley 1896, p. 23). Nevertheless, Seeley did attempt to identify anatomical features such as bones and teeth within the embryos—though he did so with extreme circumspection. These possible organic structures merit close inspection.

*Placenta.* A 'smooth film of hard clay' over parts of the specimen was considered by Seeley to have 'much the aspect of a defining membrane of a placenta-like character' (1896, p. 20). This apparently refers to the greasy lustre on the embryos and on some intervening areas of shale. The lustre is almost certainly artificial, for it is easily reproduced by gently rubbing a finger-tip over a fresh patch of the shale.

*Median dorsal ridge.* 'Each of the four principal specimens is characterized by a median longitudinal ridge or blunt angle which extends down . . . what I regard as the dorsal surface; corresponding in position to the neural spines of the vertebrae' (Seeley 1896, p. 21). The ridge is visible in unweathered and undamaged portions of the embryos, though it is sometimes very faint. Nowhere is there any trace of organic structure in, or beneath, the ridge; and there is no evidence to confirm that the ridge is 'dorsal' in position.

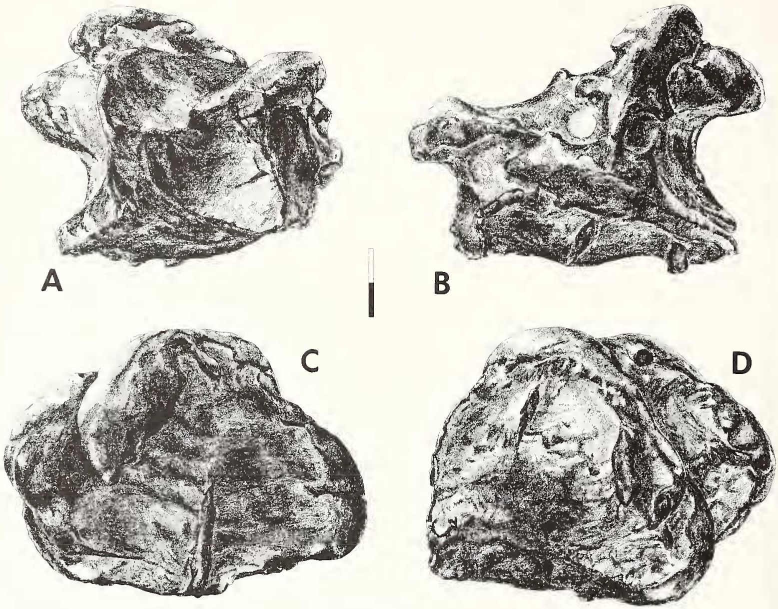
*Sclerotic ring.* On the right side of the 'head' in embryo 1 is a shallow oval pit which was tentatively identified by Seeley as the orbit. This pit originally contained 'a scale with a radiated structure, which had the appearance of being a sclerotic circle of bones about the eye', but this was subsequently lost from the specimen (Seeley 1896, pp. 22, 24). The supposed orbit is now floored by a paper-thin layer of finely crystalline pyrite, which is overlain near the anterior margin by a patch of shale containing flecks of white calcite. The floor of the orbit appears to be featureless—though Seeley maintained that there was possibly 'some evidence of a radiating structure' (1896, p. 25). The 'radiated scale' described by Seeley is unlikely to have been a sclerotic ring, because it was originally applied to the concave floor of the 'orbit': sclerotic plates are usually embedded in the lateral half of the eyeball, and therefore tend to be arched outwards from the orbit (Walls 1942). If the 'radiated scale' were a series of sclerotic plates it would be necessary to suppose that the entire eyeball had been squashed flat in the embryo; and if the eyeball had been squashed or ruptured it would be reasonable to expect evidence of similar distortion in other regions of the soft-bodied embryos. In any case, it seems improbable that delicate and superficial ossifications would have been preserved, while deeper and presumably more robust bones were obliterated. I suspect that the 'radiated scale' was no more than a thin vein of calcite, resembling similar veins in other parts of the nodule.

*Scapula.* The 'left forelimb' of embryo 2 is truncated by a fracture, behind which 'the dorsal aspect of the limb appears to include a surface bone in the position of the ascending process of the plesiosaurian scapula' (Seeley 1896, p. 23). I can find no trace of bone in this area; there is a slight surface irregularity postero-dorsal to the 'limb', but this is not particularly reminiscent of the outline of a scapula. Moreover, the ascending ramus of the plesiosaurian scapula is situated in front of the glenoid cavity, and not behind it.

*Muscle segments.* According to Seeley, 'there appear to be some faint indications of transverse segmentation like that of muscles, in the region of the neck in the specimen No. 1, and in the dorsal region in specimen No. 2' (1896, p. 23). There seems to be no trace whatsoever of segmental structure in embryo 2. Much of the 'neck' of embryo 1 has an irregular, flaky, and pitted surface. In its posterior third the right side of the neck carries a series of deep needle-marks which extend into the adjoining shale; it is improbable that these would be taken as evidence of segmentation, even at a casual glance. Above this line of needle-marks is a smooth area which proves, on close inspection ($\times 50$), to carry an ornament of extremely fine, straight, and parallel scratches. These microscopic scratches were most probably produced with a mild abrasive: they are so regular in depth, spacing, and orientation (antero-dorsal to postero-ventral) that they cannot have been produced individually, and they are so unvaryingly straight and parallel that they do not seem to be a natural feature. Over all, there is no clear evidence of segmentation in any of the embryos.

*Mandible and teeth.* 'It is possible . . . that the lower jaw may be indicated in the film of clay, which is imperfectly preserved beneath the head [of embryo 1], and that some small badly preserved white spots arranged in linear succession are indications of teeth' (Seeley 1896, p. 24). The 'head' of embryo 1 meets the shale matrix without any indication of a separate mandible. Alongside the right surface of the 'head' is a string of tiny white spots, each about 0·15 mm in diameter; these are blebs of calcite similar to those scattered throughout the specimen, and their roughly linear arrangement seems to be fortuitous.

*Skull roofing bones, external nostrils, and parietal foramen.* All these features were tentatively identified by Seeley on the 'head' of embryo 1. The surface of the 'head' is marked with a random assortment of pits, furrows, and scratches, all of which seem to be preservational and weathering effects comparable to those in other parts of the embryos. None of the grooves or scratches can justifiably be regarded as a mid-line suture between skull roofing bones, and none of the pits can be matched up into a pair that could convincingly represent the external nostrils.

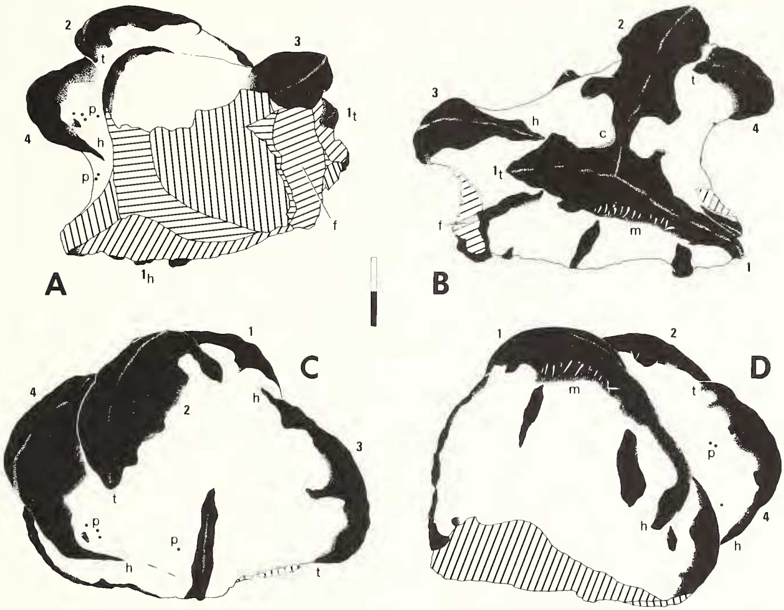



TEXT-FIG. 1. Four views of nodule from the Upper Liassic of Whitby, Yorkshire, showing supposed plesiosaur embryos. BM(NH) R.3585; scale indicates 2 cm.

Other anatomical features of the embryos (heads, necks, bodies, tails, and limbs) were identified by Seeley purely on the basis of their shape and their position. In summary, there seems to be no evidence of organic structure in any of the supposed embryos.

## DISCUSSION

There are several reasons why the specimen is unlikely to be a cluster of plesiosaur embryos. First, it lacks any definite organic structure. Some of the anatomical features identified by Seeley (1896) are no more than surface irregularities, scratches, pits, and similar weathering effects (e.g. 'scapula', 'nostrils', and 'skull bones'); other such features are patches of calcite (e.g. 'teeth') or artifacts (e.g. 'placenta'). Second, the supposed embryos show differences in shape and proportions. Seeley accounted for this variation by suggesting that the embryos were in different stages of development, but this is not a particularly convincing explanation. Where embryos, neonates, or juveniles of reptiles are preserved as natural groups of fossils the siblings are invariably in the same state of development—as, for example, in ichthyosaurs (Hauff 1921; Hoffmann 1958; Urlichs, Wild, and Ziegler 1979), in nothosaurs (Halstead 1969), and in ornithopod dinosaurs (Horner and Makela 1979). Next, and most important, it is highly improbable that soft-bodied embryos could have been preserved 'in the round' in a shale matrix. Sediment compaction usually ensures that soft organisms are preserved in a partly or completely flattened state, yet the supposed plesiosaur embryos form a




TEXT-FIG. 2. Diagrammatic interpretation of text-fig. 1. Shale matrix unshaded, and supposed plesiosaur embryos (here regarded as sediment-filled crustacean burrows) indicated by solid shading. Fracture surfaces indicated by oblique shading. Supposed embryos (= burrows) are numbered following Seeley (1896), and each has its 'dorsal ridge' (= groove in burrow floor) shown schematically. Abbreviations: c—cut surface; f—area from which a fragment was detached to provide thin sections for Seeley (1896); h—'head' of supposed embryo (= part of shaft leading to burrow chamber); m—needle-marks (shown schematically) along the side of supposed embryo 1 (= burrow 1); p—spots indicating location of possible faecal pellets; t—'tail' of supposed embryo (= burrow termination). Scale indicates 2 cm.

spheroidal mass which is not obviously flattened or distorted. If this specimen were a group of embryos it would be necessary to suppose that it had been enclosed in a syngenetic or diagenetic concretion (following terminology of Pantin 1958), or that the embryos had been mineralized before compaction of the surrounding sediment. The specimen was clearly not enclosed in a concretion, for the supposed embryos are separated and overlain by soft shale; and it seems unlikely that embryos could have been mineralized *in utero* or in an unconsolidated shale matrix. In rare circumstances human embryos are known to undergo spontaneous abortion and calcification—to become 'stone babies' or 'lithopedia' (Halstead and Middleton 1972)—but there are no reports of comparable abnormalities among fossil vertebrates. It seems a very remote possibility that the supposed plesiosaur embryos could be reptilian equivalents of 'lithopedia'.

What, then, is the most probable identity of the specimen? It is quite unlike a concretion, or even an aggregate of small concretions. Some parts of the supposed embryos bear a resemblance to coprolites, but the specimen as a whole seems too complicated in structure to be a mass of coprolites or of intestinal fillings. Each of the supposed embryos is a multi-lobed object (with several lobes representing the 'tail' and the 'limbs'), whereas individual coprolites are normally sausage-shaped, spiral, fusiform, or pellet-like objects which are not developed into lobes (see Amstutz 1958, and many references therein). Nor does the specimen resemble any known endocranial cast of a vertebrate (Edinger 1929; Jerison 1973).

From a review of literature dealing with trace fossils and problematica I strongly suspect that the supposed plesiosaur embryos are actually the sediment-filled burrows of a crustacean—most probably a shrimp resembling those of the decapod superfamily Thalassinoidea. The thalassinoid shrimp *Callianassa* excavates distinctive burrow systems in modern marine sediments (see Braithwaite and Talbot 1972), and comparable burrows have been reported as far back as the Triassic (Fiege 1944; Ireland, Pollard, Steel, and Thompson 1977) and even the Upper Carboniferous (Warme and Olson 1971; Chamberlain and Clark 1973). Fossil thalassinoid burrows are often referred to the ichnogenus *Thalassinoides* (reviewed by Bromley and Frey 1974); they vary considerably in size and architecture, according to the specific identity of the burrower (e.g. see Braithwaite and Talbot 1972) and to the nature of the sediments (e.g. see Bromley 1967). Nevertheless, it is possible to give a brief generalized description (based on Weimer and Hoyt 1964; Glaessner 1969; and sources mentioned above). A thalassinoid burrow system comprises one or more chambers (or tunnels) opening to the sea floor by a steeply inclined shaft which is wide enough to permit free passage of the burrower. A second shaft, which is often narrower and distinctly tapered, extends to the surface from another part of the chamber system. The shrimp occupies one of the chambers and creates a current by movements of its swimmerets; water enters the wider shaft and is expelled through the narrower shaft, often serving to flush out faecal pellets. The chamber occupied by the shrimp is big enough for the animal to turn round completely in somersault fashion. The various chambers are connected by constricted passages, and the shrimp may excavate several short galleries from the sides of a chamber. In some cases the chambers occur at random, while in others they may form a spiral or radial pattern. In soft sediments the shafts may be deep, and there may be many chambers excavated at several horizons; in more resistant sediments the burrow system may comprise little more than ramifying tunnels confined to a preferred horizon. When such burrow systems are encountered as fossils they are commonly filled with minerals or sediments which differ from the surrounding rock.

The supposed plesiosaur embryos are readily interpreted as thalassinoid burrow fillings (see text-fig. 2). Their ovoid 'bodies' seem to represent a series of chambers arranged in a roughly radial pattern, while their 'necks' may be identified as steeply inclined shafts connecting chambers at different levels or leading towards the former sea floor. Some of the 'necks' have a distinctly tapered tip and may be regarded as excurrent shafts. There is no trace of a broader incurrent shaft, but this would most likely have been situated in the region of the badly damaged 'North Pole'. The 'tails' are probably burrow-ends, which are 'usually somewhat conical, coming to a blunt point' in thalassinoid burrows from the English Chalk (Bromley 1967, p. 162). The 'limbs' of the supposed embryos may be identified as short galleries developed from the walls of the main chambers.

Nearly all major features of the supposed embryos can be matched in thalassinoid burrows of one sort or another. And several other facts would seem to confirm that Seeley's specimen is a thalassinoid burrow system. The shale matrix of the specimen contains a few tiny spheroidal objects (about 0·5 mm in diameter) which may possibly be faecal pellets flushed out from the interior of the burrow; several of these occur in the shale around embryo 4. Next, the invertebrate fauna of the Whitby Lias includes a variety of small decapod crustaceans, and some of these (*Glyphea* spp. and *Eryma* sp.) are similar in size and configuration to modern burrowing shrimps. Blake listed seven species of crustaceans from the Whitby Lias, and mentioned that 'numerous crustacean claws occur in many zones' (1876, p. 429). *Glyphea* and *Eryma* are not close relatives of the living thalassinoid shrimps, but 'it must be remembered that similar burrows indicate possibly similar body shape and behaviour, not systematic identity of the burrower' (Glaessner 1969, p. 430). Bromley and Frey (1974) listed many crustaceans know to construct burrows of *Thalassinoides* type, and among these were Jurassic shrimps of the superfamily Glypheoidea (Sellwood 1971; Bromley and Asgaard 1972).

It is possible, then, that one or more of the crustaceans reported from the Whitby Lias (most probably *Glyphea* spp.) may have constructed thalassinoid burrows. Remains of crustaceans are rarely found inside thalassinoid burrows, probably because the animals left their burrows to moult (see Glaessner 1969, p. 434). Finally, burrows are abundant at some horizons in the Whitby Lias. The distribution of these burrows was studied by Morris (1979), who did not specify the occurrence of *Thalassinoides* but mentioned that the trace fossil assemblages were dominated by *Chondrites*. In other sedimentary settings *Chondrites* may be associated with another trace fossil, *Gyrolithes*, which is sometimes linked with *Thalassinoides* to form a single burrow system (Bromley and Frey 1974). This very indirect evidence may hint at the existence of thalassinoid burrows in the Upper Lias at Whitby; such an occurrence would not be surprising, since *Thalassinoides* is widespread in the British Lower Lias (Sellwood 1970; Sellwood, Durkin, and Kennedy 1970). It is worth noting that Morris found *Chondrites* restricted to a 'normal' shale facies—'a homogeneous bioturbated sediment often containing sideritic nodules or horizons' (1979, p. 117). Morris studied only the lower part of the Toarcian succession at Whitby (as high as the Hard Shales), so that his 'normal' shales are in fact represented by the Grey Shales. It has already been deduced, on other grounds, that the supposed plesiosaur embryos came from the Grey Shales or from the Cement Shales (which were not considered by Morris). In other words, it seems probable that Seeley's specimen came from a 'normal' shale horizon in which burrows are abundant.

In summary, the nodule interpreted by Seeley (1896) as a group of plesiosaur embryos bears a strong resemblance to a system of thalassinoid burrow fillings. Crustaceans known from the Whitby Lias may well have included forms capable of excavating such burrows; and burrows (though not specifically identified as thalassinoid) are abundant in the 'normal' shale facies from which the nodule is likely to have come. The specimen has only one structural feature that I have been unable to match in any other thalassinoid burrow: this is the distinct 'dorsal ridge' noted by Seeley. If the specimen is interpreted as a burrow system this 'dorsal ridge' will actually represent a longitudinal groove in the floor of each burrow chamber. It is reasonable to suppose that this groove was produced by the appendages or the telson of the crustacean inhabitant.

Thalassinoid burrow fillings have commonly been mistaken for quite different objects; Bromley reported (1967, p. 158) that thalassinoid burrows of Upper Cretaceous age have been interpreted as benthonic algae, plant roots, sponges, solution channels, concretions, and trace fossils of unidentified marine organisms. Seeley's misinterpretation is all the more understandable when one considers that his specimen had been 'improved' by artificial means. Parts of the supposed embryos seem to have been smoothed off and polished with a mild abrasive, leaving a microscopic pattern of unnaturally straight and parallel scratches. And in places it appears that the main burrow chambers (or embryo 'bodies') have been trimmed to a more suggestive shape by removal of some side-galleries (which would otherwise have remained as rather puzzling supernumerary 'limbs'). Such trimming is apparent along the right side of embryo 1, where there is a series of deep needle-marks. These marks extend from the fossil *into* the shale matrix, whereas needle-marks produced in normal preparation would extend in the opposite direction. Either this work with a needle was intended to remove portions of the fossil, or it was an unbelievably clumsy attempt at preparing the specimen. Next, the suitably constricted appearance of the 'neck' in embryo 2 (text-fig. 2B) is due partly to the fact that it has been cut down with a knife-blade or similar instrument. The cut surface is easily visible; it is flat and sharp-edged, in contrast to the irregular and broadly rounded surfaces elsewhere. Finally there is evidence of a much coarser, but none the less effective, 'improvement': several hammer blows in the region of the 'North Pole' removed any trace that might have existed of an incurrent shaft leading to the burrow system. It is not altogether surprising to discover these alterations to Seeley's specimen, for many such 'improved' or 'repaired' fossils are known to have come from the dealers at Whitby (see, for example, Blake 1876, p. 428; Dance 1976, p. 103).

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